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ROAD MORTALITY OF DRAGONFLIES (ODONATA) IN A  
GREAT LAKES COASTAL WETLANDSamuel Keith Riffell<sup>1</sup>

## ABSTRACT

Although road mortality of vertebrates has been well studied, road mortality of invertebrates has rarely been studied or considered in management scenarios. Mackinac Bay is an extensive coastal wetland in northern Michigan. It is bordered by a two-lane paved highway that separates the marsh, where dragonflies defend territories and breed, from the adjacent forest where dragonflies forage and rest. During mid-summer of 1997, daily collections of dragonfly corpses from the road and road edge were used to estimate daily mortality rates and sex ratios among casualties. Daily mortality was highly variable, ranging from 10 to 256 casualties per kilometer. Sex ratios among casualties were generally male-skewed (60% or higher). Life-history differences between the sexes present a parsimonious explanation for male-specific mortality. Mortality was even or female-skewed for some species, and impacts of road mortality may be more severe in populations where mortality is female-skewed. More research about the effects of roads on dragonflies is warranted because dragonfly populations are small relative to many invertebrates and are restricted to wetland habitats which are being degraded or destroyed in many regions.

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Wildlife mortality from collisions with motor vehicles along roads is a common phenomenon and a serious management concern. In some regions, road-kills are the primary source of mortality for large mammals (Lalo 1987, Harris and Gallagher 1989), and road-kills can be a substantial source of mortality for birds (Forman 1995, Ashley and Robinson 1996), amphibians (e.g. van Gelder 1973, Fahrig et al. 1995, Ashley and Robinson 1996), and reptiles (Rosen and Lowe 1994). Over time, road mortality can create genetically disjunct subpopulations (Merriam et al. 1989), depress population sizes (Rosen and Lowe 1994, Fahrig et al. 1995), and alter the size- and age-structure of populations (Rosen and Lowe 1994). Consequently, road mortality data have been incorporated into predictive models (e.g. grizzly bear; Doak 1995), and management schemes (e.g. road underpasses for Florida panthers; Harris and Gallagher 1989) for many vertebrate species. However, even the most basic data about road mortality is exceedingly scant for aquatic invertebrates as well as terrestrial invertebrates (see Table 1 for a summary) despite anecdotal evidence that extremely high numbers of invertebrates can be killed on roads.

The importance of road mortality in aquatic invertebrates has most likely been ignored because of their life-history traits. Most groups of aquatic in-

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Table 1. Road mortality rates for invertebrates from other studies with selected rates from this study for comparison.

Invertebrate Taxon	Study Duration	Sampling Events	# Corpses	Road Length	Mortality Rate
PUBLISHED MORTALITY RATES					
Beckemeyer (1996)					
Odonata: <i>A. junius</i>	1 day	1	9	~ 0.5 km	45.00 / km / day <sup>a</sup>
Seibert and Conover (1991)					
All Insecta	14 months	50	1069	1.6 km	13.36 / km / day <sup>b</sup>
All Odonata	14 months	50	22	1.6 km	0.28 / km / day <sup>b</sup>
Munguira and Thomas (1992)					
All Butterflies	44 days	4	144	1.2 km	30.00 / km / day <sup>c</sup>
DRAGONFLY MORTALITY RATES AT MACKINAC BAY					
All Odonata	42 days	26	1140	0.5 km	87.69 / km / day
<i>L. quadrimaculata</i>	42 days	26	312	0.5 km	24.00 / km / day
<i>E. spingera</i>	42 days	26	199	0.5 km	15.31 / km / day

<sup>a</sup>Converted from an estimated 72 per mile of 4 lane highway based on sampling ~ 0.5 km of a single lane (see Beckemeyer 1996).  
<sup>b</sup>Calculated assuming each of the 50 sampling events represents 24 hours of mortality.  
<sup>c</sup>Calculated assuming each of the 4 sampling events represents 24 hours of mortality. However, Munguira and Thomas (1992) demonstrated that corpses did not disappear after 2 weeks time, and assumed the 144 carcasses represented the entire 44 days of mortality. Using this assumption, the mortality rate would be much lower (2.72 km / day).

sects with winged adult stages are highly fecund with naturally high mortality (Wallace and Anderson 1996), and have a synchronized emergence of short-lived adults which fly primarily at night (Trichoptera caddisflies; Wiggins 1996) or breed in mass swarms (e.g. Ephemeroptera mayflies; Edmunds and Waltz 1996). A common assumption is that road mortality of adults has little potential to impact population dynamics of a species with this combination of life-history traits. This assumption, however, has not been tested, and not all groups of aquatic insects (i.e. Odonata) share these traits.

Dragonflies differ from many groups of aquatic insects in several ways. Dragonfly populations are relatively small compared to other aquatic invertebrates, and emergence of adult dragonflies is usually over a period of weeks or even a month or more (Corbet 1962). Adults are long-lived (up to 10 weeks; Corbet 1980) and reproductively active for a large portion of that time, and flight occurs primarily during daylight hours. Consequently, mortality from collisions with vehicles may affect dragonfly populations more severely than other aquatic insect groups. Coupled with the destruction and degradation of wetlands that is occurring in many regions, the effect of road mortality on small or disjunct populations of dragonflies could be substantial.

I investigated the extent, species composition and sex ratio of road-killed adult dragonflies at a freshwater coastal wetland along the northern shore of Lake Huron. A major two-lane highway borders the wetland, separating the upland forest from the wetland itself. Because dragonflies, like most aquatic insects, depend on terrestrial habitat during the adult part of their life cycle (Wallace and Anderson 1996), they must cross the highway repeatedly to access the different parts of their required habitat. This situation is ideal for investigating road mortality in dragonflies and collecting information which will be important for guiding wetland management plans and directing future research.

## MATERIALS AND METHODS

**Study Area.** Mackinac Bay is located between the towns of Hessel and Cedarville in the eastern Upper Peninsula of Michigan immediately adjacent to a two-laned, paved highway (M-134). Mackinac Bay contains an extensive coastal wetland typical of the region. The vegetation of the wet meadow portion of the wetland was predominately tussocks of *Carex stricta*, *Carex aquatilis* and *Calamagrostis canadensis* interspersed with pockets of standing water and shrubs. The wet meadow then graded into homogenous stands (without tussocks) of *Carex lasiocarpus*. *Scirpus acutus* interspersed with patches of *Typha angustifolia* (D. M. Albert and T. M. Burton, unpublished data), *Pontederia cordata*, and floating vegetation (*Nuphar* sp. and *Potamogeton* sp.) dominated the deeper-water portions of the marsh. Two small streams run through the marsh and empty into Mackinac Bay.

The road (M-134) was a two-laned, asphalt highway approximately parallel to the northern coast of Lake Huron in the eastern Upper Peninsula of Michigan. It was adjacent to the coastal wetland at Mackinac Bay. The highway ran parallel to the junction of the wet meadow and the forested part of the wetland such that it was bordered on the north by cedar and tamarack forest and to the south by the wetland. Traffic volume during 1997 along this portion of M-134 was estimated at 5743 vehicles per day (Michigan Department of Transportation 1998, unpublished data).

**Dragonfly Sampling.** I collected adult dragonflies which had been killed along M-134 at Mackinac Bay by walking a marked, 500 m segment of the

highway which directly bordered the wetland. During each visit, I walked up one side of the road and down the other. I collected dragonfly corpses off the highway, off the gravel verge, and out of the bordering grass. I collected corpses on 26 different days between 27 June 1997 and 8 August 1997. Because I did not sample throughout the entire summer, early and late summer species were under-represented. All collecting was done between 1700 and 1900 EST. Dragonflies were identified to species level and sexed to the extent that the condition of the specimen allowed. Identifications were made using keys (Walker 1953, Needham and Westfall 1955, Walker 1958, Walker and Corbet 1975) or by comparison with reference specimens.

**Statistical Analysis.** I calculated daily mortality rate as the mean number of corpses collected per sampling day per kilometer for each species. The section of the highway used for collecting was 500 m; thus, daily mortality was equal to twice the number of corpses collected on a particular day. Because dragonfly densities are not constant, but rather peak towards the middle of the adult flight period, I also calculated "peak daily mortality rate." This value was the mean of the three sampling days with the highest number of casualties and estimated the maximum rate of mortality at each species' peak density.

It is very possible that my sampling protocol produced overestimates of mortality rates because I did not always sample on consecutive days. Munguira and Thomas (1992) found that butterfly corpses remained on the road verge for over two weeks, and for some sampling events in my study, more than 24 hours had elapsed since my previous sampling event. Thus, corpse counts from those days may have represented the cumulative mortality over several days since the previous sampling event which would result in overestimates of actual daily mortality. On two occasions, I left 10 marked specimens of *Aeshna canadensis* Walker and *Dorocordulia libera* (Selys) on the highway verge, and, on both occasions, none of the 10 specimens were found 24 hours later. Also, estimates of mortality from days when > 24 hours had elapsed since the previous collection were not significantly greater than estimates from sampling events when only 24 hours had elapsed. This evidence suggests that longevity of corpses did not cause overestimates of daily mortality rates in this study.

It is also possible, however, that I have underestimated mortality for two reasons. First, the dry, sunny conditions along the highway verge resulted in corpses which dried in a matter of hours. These dried corpses were very light, and many were likely blown off the verge by coastal winds which were common (S. Riffell, personal observation). These corpses would not have been collected during the sampling events. Second, although Munguira and Thomas (1992) indicated that very few, if any, butterfly corpses were carried off in radiators or grills, my observations at Mackinac Bay suggest that at least some dragonfly corpses were removed from the study area in this manner.

I calculated the sex ratio of casualties as the percent of the corpses that were male. Corpses too damaged to confidently determine sex were not included in this calculation. To test if sex ratios among casualties were different from 1.00 (i.e. 50% male, 50% female), I used a logarithm-based G-statistic (Zar 1984). G-statistics were not calculated if <10 specimens of a particular species or taxonomic group were collected.

## RESULTS

I collected a total of 1140 dragonfly corpses along the highway bordering the Mackinac Bay wetland. Corpses were from seven different families and

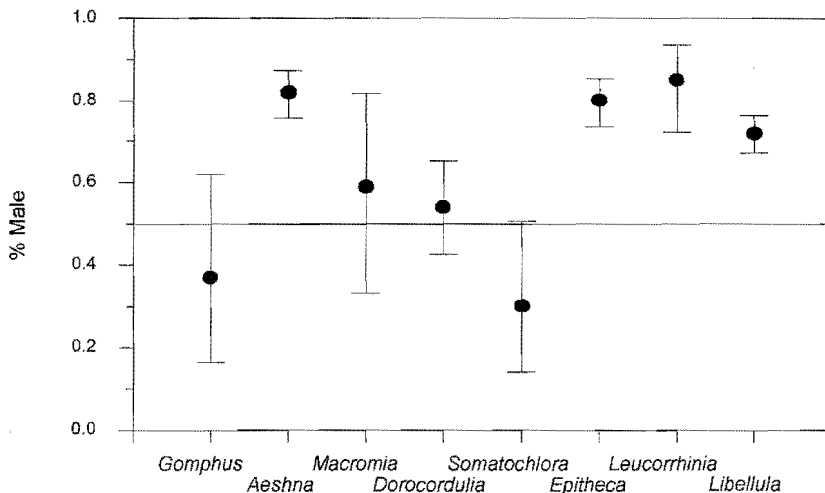


Figure 1. Sex ratios (% male) of road casualties at Mackinac Bay for selected genera of dragonflies. Error bars represent  $\pm 1$  SE (according to Zar 1984).

25 different species. Just over two-thirds of the corpses were comprised of just four species: *Libellula quadrimaculata* Linn., *Aeshna canadensis*, *Epithea spinigera* Selys, and *Dorocordulia libera*.

**Daily Mortality Rates.** Mean daily mortality of all Odonata was 87.69 dragonfly casualties per kilometer. The highest number of casualties on a single day was 256 corpses/km; the lowest was 10 corpses/km (Appendix A). For individual species, *Libellula quadrimaculata* had the highest mean daily mortality rate (24.00 km/day [Table 1, Appendix A]). For most species and higher taxonomic groupings, mortality rates were highly variable.

**Sex Ratio of Casualties.** Overall, 73% of the road casualties were male (Appendix B), but the sex ratio varied among genera (Figure 1). Mortality was significantly male-skewed for *Aeshna* (82% male;  $P < 0.001$ ), *Epithea* (80%;  $P < 0.001$ ), *Leucorrhinia* (85%;  $P < 0.001$ ), and *Libellula* (72%;  $P < 0.001$ ) while mortality of *Somatochlora* (30%;  $P < 0.050$ ) was significantly female-skewed. Mortality of *Macromia* (59%), *Dorocordulia* (54%) and *Gomphus* (37%) were not significantly sex-skewed (Figure 1; Appendix B). At the species level, 20 of the 25 species collected had male-skewed mortality, and this was statistically significant for six species: *Aeshna canadensis*, *Anax junius* (Drury), *Epithea spinigera*, *Leucorrhinia* sp., *Libellula julia* (Uhler), and *L. quadrimaculata*. Casualties were female-skewed in four species, but only one (*Somatochlora walshi* (Scudder)) was significant (Appendix B).

## DISCUSSION

**Daily Mortality Rates.** Daily mortality rates of dragonflies at Mackinac Bay were larger than published rates for other invertebrate taxa (Table 1), and agree with the high mortality rate of *Anax junius* (Drury) reported by Beckemeyer (1996 and Table 1). Such high rates of mortality were not sur-

prising because of the different habitats that dragonflies require during different stages of the adult lifespan. Immediately after emergence, adults of most species of dragonflies leave the wetland and go to nearby terrestrial habitats (forests, meadows), where they shelter and feed (Corbet 1962). When they reach reproductive maturity (typically a few weeks; Corbet 1980), they return to the wetland to defend territories, copulate, and oviposit. At Mackinac Bay, this highway separates the terrestrial forest almost completely from the wetland, and nearly all movement between the two habitats requires that dragonflies cross the highway. Such positioning of the highway maximizes the potential for dragonfly crossings and, hence, fatal collisions.

Others have described a similar phenomenon during amphibian breeding migrations (van Gelder 1973, Fahrig et al. 1995), where an alarming percentage of a population may be killed when the amphibians must cross roads to reach their breeding habitats (van Gelder 1973). Dragonflies differ from amphibians, however, in that return trips for breeding are undertaken daily, or more often by some individuals. For dragonflies, the potential for road mortality exists throughout the reproductive period of the organism, not just the initial migration period. Biologists and planners alike should consider the effects of road mortality on dragonfly populations and the effects of road position on mortality rates. For small or isolated populations, such high rates of mortality could potentially threaten population persistence, and further research about the effects of road mortality on population dynamics is sorely needed to accurately gauge this threat.

My estimates of daily mortality were high, but extremely variable from day to day (see Appendix A), which reflects the wide array of factors which can impact the actual number of collisions that occur. In theory, the number of insect-car collisions could be influenced by (1) dragonfly density and behavior and (2) traffic density and speed (van Gelder 1973, Fahrig et al. 1995). Both dragonfly and traffic characteristics can be influenced by a myriad of secondary factors. For instance, dragonfly density can be influenced by the amount and quality of the wetland habitat (e.g. presence of fish decrease Odonate abundance; Batzer and Wissinger 1996), the species composition of dragonfly community (i.e. some species may be more densely populated), and dragonfly activity level which is in turn a function of weather, temperature, and behavior. Traffic density and speed could be influenced by time of day (e.g. work traffic), time of week (e.g. recreational weekend traffic), visibility, characteristics of the road (e.g. paved vs. nonpaved) and the size and characteristics of the communities connected by the roadway in question. Unfortunately, little is known about many of these factors, so predicting even relative mortality rates in other locations is not possible. Research about how these factors interact to influence road mortality rates in a variety of habitats and settings is necessary to accurately understand the effects of road mortality on dragonfly populations.

Although the most abundant species generally had the highest mortality rates (S. Riffell, personal observation), quantitative data about the background densities of adult dragonflies at Mackinac Bay was not collected. Thus, it is not possible to determine the percent of total mortality of adult dragonflies that was caused by vehicular collisions, or to make any definitive conclusions about what effects road mortality could have on population dynamics. Also, one cannot make inferences about the relative susceptibilities of particular species or taxonomic groups. Some species, such as *Libellula julia* and *Gomphus* sp., were often seen basking on the road itself, and it would seem that they would suffer greater per capita mortality than other species which did not exhibit such behavior, but such data are lacking. Future studies could use visual estimates of background population size (e.g.

transect counts), make detailed observations of flight behavior and/or road crossing success, or mark individuals and estimate mortality as percentage of marked individuals among the casualties.

**Sex ratios of Casualties.** Although males usually comprise only 40 - 50% of the population at emergence (Corbet 1980), over 70% of all dragonfly corpses were males (Appendix B). This is strong evidence that road mortality at Mackinac Bay was truly male-specific. However, it would be premature to conclude that males are actually more *susceptible* while crossing roads than are females. In most Odonata, males spend most or all of their reproductive lives at the wetland breeding sites defending territories, whereas females spend far less time at breeding sites (Corbet 1962; Hamilton and Montgomerie 1989), often being absent for several days after successful oviposition (Michiels and Dhondt 1991). At the Mackinac Bay wetland, males would be required to make at least two highway crossings per day, and females far fewer. Male-skewed mortality at Mackinac Bay is at least partly due to the greater number of males crossing the highway and the higher crossing frequency per male. However, whether or not males have a different probability of survival *per crossing* than females is not known. Estimating sex differences in crossing survival would require detailed observations of crossing events or recovery of marked individuals.

Conservationists might conclude that road mortality would have little effect on the reproductive output of a population because most of the casualties were males. However, this generalization would be unwise because the sex ratios of casualties were even or actually female skewed for some species (e.g. *Somatochlora* sp., Figure 1 and Appendix B). Qualitatively, mortality of the most abundant species at the wetland (e.g. *A. canadensis*, *L. quadrimaculata*, *Leucorrhinia* sp.; based on larval abundances; T. Burton, unpublished data) was the most heavily male-skewed, while mortality of less abundant species (e.g. *Gomphus spicatus* Hagen, *Macromia illinoensis* Walsh, *Somatochlora* sp.) was less male-skewed or even female-skewed.

Two mechanisms may account for this pattern. First, increased abundance of males may increase the number of territorial disputes among males, thus increasing their road crossing frequency (S. Riffell, personal observation). This would increase male mortality at high densities. Second, lower densities of males decreases the probability that a female can breed successfully (Michiels and Dhondt 1991), and females would have to make additional road-crossings until they are successful. This would increase female mortality at low densities. Although these ideas are speculative and based on qualitative observations, I have presented them for the sake of fostering further discussion and research. Sex differences in road mortality among species could also be a result of differences in the sex ratio of individuals at the wetland, differential flight abilities between sexes in some species but not others, or other factors. Identifying causes of sex-skewed mortality is important because female-specific mortality could have a severe impact on reproductive output, and thus population persistence, for species with small and/or isolated populations.

**Implications for Conservation.** It is clear that large numbers of a wide array of dragonfly species can potentially become casualties of vehicular collisions. For small or isolated populations such as the rare Hine's Emerald (*Somatochlora hineana* Williamson), losses from road mortality take on greater importance because small populations are particularly susceptible to extinction. Additionally, road mortality of congeneric *Somatochlora* species was female-skewed at Mackinac Bay, and the impact of female-skewed mortality on populations of Hine's Emerald has not been investigated. Predicting the effects of road mortality on dragonfly populations and conserving road-



impacted populations will be difficult without further understanding of the causes and effects of road mortality in dragonflies. Priorities for research should focus on: (1) determining the percent of total adult mortality that is caused by vehicular collisions; (2) identifying the factors which affect crossing survivorship and mortality rates; and (3) determining the effects of sex-skewed mortality on the sex composition and reproductive potential of dragonfly populations.

Dragonfly road mortality would be minimized if no additional roads were constructed in or near dragonfly habitats. When roads must be constructed, careful consideration of road placement could ameliorate potential impacts on dragonfly populations. Roads which are placed in critical breeding habitat (i.e. actual wetland) or which separate different habitats used by dragonflies (i.e. splitting forest and wetland) should not be constructed if reasonable alternatives exist. Relative to other flying insects, dragonflies are extremely quick and agile flyers (Brodsky 1994). It is very possible that merely reducing traffic speeds in critical areas may significantly reduce insect-vehicle collisions, but this idea has not been tested. Other options include constructing temporary tunnels over sections of roads with high mortality to prevent dragonflies from crossing at car level or resting on the road surface. More research should be conducted, however, to determine the true impact of road mortality on dragonfly populations and to assess the effectiveness of proposed management options before time- and resource-consuming conservation efforts are implemented.

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Appendix A. Mean daily road-mortality rates (# of corpses) and peak mortality rates (per kilometer per day) of adult dragonflies at Mackinac Bay, Michigan during summer 1997.

Species	Daily Mortality Rates		Peak Mortality Rates*
	Mean $\pm$ 1 SD	Range	Mean $\pm$ 1 SD
<b>CALOPTERYGIDAE</b>			
<i>Calopteryx aequabilis</i> Say	0.23 $\pm$ 0.65	2.0-0.0	2.00 $\pm$ 0.00
<i>Calopteryx maculata</i> (Beauvois)	0.46 $\pm$ 1.03	4.0-0.0	2.67 $\pm$ 1.15
<b>CORDULEGASTRIDAE</b>			
<i>Cordulegaster maculatus</i> Selys	0.23 $\pm$ 0.65	2.0-0.0	2.00 $\pm$ 0.00
<i>Continued</i>			

## Appendix A. Continued.

Species	Daily Mortality Rates		Peak Mortality Rates*
	Mean $\pm$ 1 SD	Range	Mean $\pm$ 1 SD
<b>GOMPHIDAE</b>			
<i>Arigomphus cornutus</i> Tough	0.54 $\pm$ 1.33	4.0–0.0	4.00 $\pm$ 0.00
<i>Gomphus spicatus</i> Hagen	1.46 $\pm$ 2.56	8.0–0.0	6.67 $\pm$ 1.15
Unk. Gomphidae	1.85 $\pm$ 4.19	18.0–0.0	12.00 $\pm$ 5.29
Total Gomphidae	3.85 $\pm$ 5.42	18.0–0.0	14.67 $\pm$ 3.06
<b>AESHNIDAE</b>			
<i>Aeshna canadensis</i> Walker	12.15 $\pm$ 16.72	60.0–0.0	48.00 $\pm$ 12.00
<i>Aeshna interrupta</i> Walker	0.38 $\pm$ 1.13	4.0–0.0	3.33 $\pm$ 1.15
<i>Aeshna eremita</i> Scudder	0.15 $\pm$ 0.54	2.0–0.0	2.00 $\pm$ 0.00
<i>Aeshna umbrosa</i> Walker	0.15 $\pm$ 0.78	4.0–0.0	4.00 $\pm$ **
Unk. <i>Aeshna</i> sp.	1.77 $\pm$ 3.11	14.0–0.0	8.67 $\pm$ 5.03
Total <i>Aeshna</i> sp.	14.62 $\pm$ 19.48	70.0–0.0	58.67 $\pm$ 10.26
<i>Anax junius</i> (Drury)	1.62 $\pm$ 1.79	6.0–0.0	5.33 $\pm$ 1.15
<i>Basiaeschna janata</i> (Say)	0.31 $\pm$ 0.74	2.0–0.0	2.00 $\pm$ 0.00
<i>Gomphaeschna furcillata</i> (Hagen)	0.46 $\pm$ 1.17	4.0–0.0	3.33 $\pm$ 1.15
Total Aeshnidae	17.00 $\pm$ 18.85	72.0–0.0	60.00 $\pm$ 11.14
<b>MACROMIIDAE</b>			
<i>Macromia illinoensis</i> Walsh	1.54 $\pm$ 2.85	12.0–0.0	8.00 $\pm$ 3.46
<b>CORDULIIDAE</b>			
<i>Cordulia shurtleffi</i> Scudder	0.46 $\pm$ 1.03	4.0–0.0	2.67 $\pm$ 1.15
<i>Dorocordulia libera</i> (Selys)	6.77 $\pm$ 7.65	24.0–0.0	22.67 $\pm$ 1.15
<i>Somatochlora franklini</i> (Selys)	0.08 $\pm$ 0.39	2.0–0.0	2.00 $\pm$ **
<i>Somatochlora walshi</i> (Scudder)	1.31 $\pm$ 1.95	6.0–0.0	5.33 $\pm$ 1.15
<i>Somatochlora williamsoni</i> Walker	0.38 $\pm$ 0.98	4.0–0.0	2.67 $\pm$ 1.15
Unk. <i>Somatochlora</i> sp.	0.38 $\pm$ 0.98	4.0–0.0	2.67 $\pm$ 1.15
Total <i>Somatochlora</i> sp.	2.15 $\pm$ 3.15	12.0–0.0	9.33 $\pm$ 3.06
<i>Epitheca spinigera</i> Selys	15.31 $\pm$ 17.44	70.0–0.0	50.67 $\pm$ 16.77
Unk. <i>Epitheca</i> sp.	1.62 $\pm$ 3.87	14.0–0.0	11.33 $\pm$ 3.06
Total Corduliidae	27.85 $\pm$ 28.05	102.0–0.0	87.33 $\pm$ 18.90
<b>LIBELLULIDAE</b>			
<i>Leucorrhinia</i> sp.	4.15 $\pm$ 6.14	18.0–0.0	16.67 $\pm$ 1.15
<i>Libellula julia</i> (Uhler)	8.15 $\pm$ 13.05	58.0–0.0	36.00 $\pm$ 19.08
<i>Libellula pulchella</i> Drury	1.54 $\pm$ 2.14	8.0–0.0	5.33 $\pm$ 2.31
<i>Libellula quadrimaculata</i> Linn.	24.00 $\pm$ 24.57	92.0–0.0	69.33 $\pm$ 19.63
Total <i>Libellula</i> sp.	33.69 $\pm$ 37.65	154.0–0.0	107.33 $\pm$ 40.46
<i>Sympetrum corruptum</i> (Hagen)	0.08 $\pm$ 0.39	2.0–0.0	2.00 $\pm$ **
<i>Sympetrum obtrusum</i> (Hagen)	0.15 $\pm$ 0.54	2.0–0.0	2.00 $\pm$ 0.00
Total Libellulidae	38.08 $\pm$ 41.37	164.0–0.0	121.33 $\pm$ 37.00
<b>TOTAL ODONATA</b>	<b>87.69 <math>\pm</math> 68.41</b>	<b>256.0–10.0</b>	<b>226.00 <math>\pm</math> 26.15</b>

\* Peak rates are the mean of the three dates with the highest mortality for that taxonomic grouping.

\*\* Standard deviations are not provided for species that were only collected on a single date.

Appendix B. Sex ratios (% male) of dragonfly casualties at the Mackinac Bay wetland during summer 1997.

Species	Males	Females	Unknown	Total	% Male	G-statistic*	P-value
<b>CALOPTERYGIDAE</b>							
<i>Calopteryx aequabilis</i>	3	0	0	3	100		
<i>Calopteryx maculata</i>	1	4	1	6	17		
<b>CORDULEGASTRIDAE</b>							
<i>Cordulegaster maculatus</i>	3	0	0	3	100		
<b>GOMPHIDAE</b>							
<i>Arigomphus cornutus</i>	6	1	0	7	86		
<i>Gomphus spicatus</i>	7	12	0	19	37	1.331	NS
Unk. Gomphidae	12	7	5	24	63	1.331	NS
Total Gomphidae	25	20	5	50	56	0.557	NS
<b>AESHNIDAE</b>							
<i>Aeshna canadensis</i>	129	25	4	158	84	76.883	<0.001
<i>Aeshna interrupta</i>	4	1	0	5	80		
<i>Aeshna eremita</i>	2	0	0	2	100		
<i>Aeshna umbrosa</i>	2	0	0	2	100		
Unk. <i>Aeshna</i> sp.	12	7	4	23	63	1.331	NS
Total <i>Aeshna</i> sp.	149	33	8	190	82	79.993	<0.001
		18					
<i>Anax junius</i>	18	3	0	21	86	11.887	<0.001
<i>Basiaeschna janata</i>	3	1	0	4	75		
<i>Gomphaeschna furcillata</i>	4	2	0	6	67		
Total Aeshnidae	174	39	8	216	82	92.479	<0.001
<b>MACROMIIDAE</b>							
<i>Macromia illinoensis</i>	10	7	3	20	59	0.532	NS
<b>CORDULIIDAE</b>							
<i>Cordulia shurtleffi</i>	3	2	1	6	60		
<i>Dorocordulia libera</i>	44	37	7	88	54	0.606	NS
<i>Somatochlora franklini</i>	1	0	0	1	100		
<i>Somatochlora walshi</i>	5	12	0	17	29	2.970	<0.100
<i>Somatochlora williamsoni</i>	1	4	0	5	20		
Unk. <i>Somatochlora</i> sp.	1	3	1	5	25		
Total <i>Somatochlora</i> sp.	8	19	1	28	30	4.615	<0.050
<i>Epitheca spinigera</i>	152	38	9	199	80	73.243	<0.001
Unk. <i>Epitheca</i> sp.	12	3	6	21	80	5.782	<0.025
Total Corduliidae	229	106	27	362	68	46.235	<0.001
<b>LIBELLULIDAE</b>							
<i>Leucorrhinia</i> sp.	44	8	2	54	85	27.438	<0.001
<i>Libellula julia</i>	71	22	13	106	76	27.168	<0.001
<i>Libellula pulchella</i>	10	7	3	20	59	0.532	NS
<i>Libellula quadrimaculata</i>	191	79	42	312	71	47.893	<0.001
Total <i>Libellula</i> sp.	272	108	58	438	72	73.158	<0.001
<i>Sympetrum corruptum</i>	1	0	0	1	100		
<i>Sympetrum obtrusum</i>	1	1	0	2	50		
Total Libellulidae	318	117	60	495	73	96.500	<0.001
<b>TOTAL ODONATA</b>	<b>753</b>	<b>286</b>	<b>101</b>	<b>1140</b>	<b>73</b>	<b>217.612</b>	<b>&lt;0.001</b>

\* Zar (1984). Statistical hypotheses were not tested if &lt; 10 individuals were collected.